

## Orthocephalization in the Postweaning Squirrel Monkey

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**ABSTRACT** Twenty male squirrel monkeys (*Saimiri sciureus boliviensis*) raised in captivity were allotted to one of the following groups: weanling control (C6) sampled at 6 months of age; young control (C24) fed ad libitum on a control diet and killed at 24 months of age; and malnourished (M24) fed ad libitum on a low-protein diet and sampled at 24 months of age. Cranial points and the lateral semicircular canals were marked. On each skull, a strict lateral telerradiograph was taken, and the lengths of the midsagittal chords and their angles with respect to the vestibular line were measured. Age changed the lengths in about 70% of the chords and more than 50% of the angles. Malnutrition arrested about 50% of the lengths, but the angles were practically not affected. It is concluded that the postweaning *Saimiri sciureus* undergoes orthocephalization according to a general pattern already observed in rodents and suggested for pongids. Postweaning malnutrition affected growth in size but not shape changes related to the orthocephalization of the *Saimiri* skull. © 1996 Wiley-Liss, Inc.

The cranial shape in rodent species evolves from a klinorrhynchal stage at birth to an orthocranial position in the adult. The face at birth is oriented anteroinferiorly with respect to the neurocranium. Next, the face is placed directly in front of the neural skeleton. This rotation of the face—called “orthocephalization”—may offer a useful nonhuman model for understanding normal and stressed growth. It is thought it may be selectively altered by experimentally induced factors.

For studying orthocephalization, skulls may be oriented according to one of the currently accepted arbitrary external frames of reference: “external” because they do not vary by eventual displacements of the specimen, and “arbitrary” since they must be based at least on three cranial points, which would not remain stable during growth. These constraints can be solved either by Finite Element methods (Moss et al., 1987a,b; Pucciarelli et al., 1987; Corner and

Richtsmeier, 1991, 1992) or by vestibular orientation, based on the horizontality of the lateral semicircular canals of the inner ear (Delattre, 1952a; Moss, 1961).

Vestibular orientation is a consistent registration system. This method differs from the ones whose reference points are placed on the exocranium. Vestibular points belong to a functional component (vestibular system of the inner ear) of the skull that varies independently from the rest of the neurocranium (Moss, 1961).

Vestibularly oriented crania from normal and stressed rats have been studied (Desombes and Fenart, 1974; Pucciarelli, 1978; Pucciarelli and Niveiro, 1981; Vilman and

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Moss, 1979), but such studies are scarce in primates. In New World monkeys, some reports have been presented on *Alouatta* (Perez, 1922) and *Saimiri* (Delattre and Anthony, 1951; Delattre, 1952b). A mandibular study on vestibularly oriented crania was also made on several platyrrhine species (Fenart and Anthony, 1967).

The present work seeks to determine (1) whether orthocephalization is evident during the postweaning growth of the squirrel monkey and, if so, (2) how this process can be altered by malnutrition, and (3) whether *Saimiri* orthocephalization may be thought of as part of a general mammalian pattern of the growth of the skull.

## MATERIALS AND METHODS

Twenty male *Saimiri sciureus boliviensis* (Cebidae) of 6 and 24 months of age were employed. The monkeys were born in captivity at the Centro Argentino de Primates (CAPRIM). After weaning (six month) the animals were allotted to one of the following groups.

Weanling control (C6): six animals immediately sampled (sixth month). Young control (C24): six animals fed ad libitum on a control diet (20% protein) from weaning to the end of the experiment (24th month). Young malnourished (M24): eight animals fed ad libitum on a low-protein (5%) diet, from weaning to the end of the experiment (24th month).

Both control and low-protein diets were prepared weekly (for details see Pucciarelli et al., 1990). After death, skulls were cleaned and both the lateral semicircular canals (LSC) and the following cranial points were marked by 0.2 mm diameter copper filaments: nasion, bregma, lambda, inion, vermillion (between the vermiform fossa and the sagittal ridge of the cerebellum), and sphenoccipitale. Each skull was held in a cephalostat and X-rayed in a strict right lateral view (1.20 m distance) according to a previously described technique (Pucciarelli et al., 1990). Additionally, the gnathion, infraorbital, prosthion, rhinion, opisthion, basion, upper and lower points of the optic foramen, inner nasion, upper point of the mandibular condyles and gonion (the last two projected on the midsagittal plane), and frontal and

parietal inflections were marked directly on radiographs. A vestibular line (VL) was traced and projected on both sides of the LSC. The spatial position of each point was calculated by a coordinate system with VL as the X-axis and its orthogonal through the mesovestibion (midpoint in the length of the LSC) as the Y-axis (Pucciarelli and Niveiro, 1981).

Midsagittal tracings were drawn between the coordinate values of the cranial points. On each tracing, lengths and angles were measured for the chords of the nasal opening, nasal bones, anterior and posterior portions of the frontal and parietal bones, upper, mid, and lower portions of the occipital squama, foramen magnum, basioccipital and basisphenoid bones, optic foramen, anterior basicranium, palatomaxillary vault, and ramus, body, and alveolar and symphyseal borders of the mandible. The origin of each angle was the parallel to the X-axis which intersected the chord (or its prolongation) to be measured. It was measured starting counterclockwise, from the nasal opening to the mandibular symphysis (Fig. 1).

The normal logarithmic transformation of the length data was performed. Next, between-group multifactor analyses of variance tests were done on each length (measured in millimeters) and on each angle (expressed in radians) variable. The comparison between controls (C6–C24) gave growth information. The comparison between the older controls and the malnourished group (C24–M24) indicated whether malnutrition acted on growth. To eliminate size differences between variables, the Relative Difference between Means (RDM) was standardized according to the following formula:

$$\text{RDM} = \frac{\bar{X}_1 - \bar{X}_2}{\bar{X}_1 + \bar{X}_2} 100$$

where  $\bar{X}_1$  = mean values from the elder controls and  $\bar{X}_2$  = mean values from the younger controls or from the malnourished group.

Since RDM shows percent values, any mean difference within each variable (length or angle) can be compared to that of any other. Statistical analyses were performed by the ARGSTAD 1.0 package, at the Centro

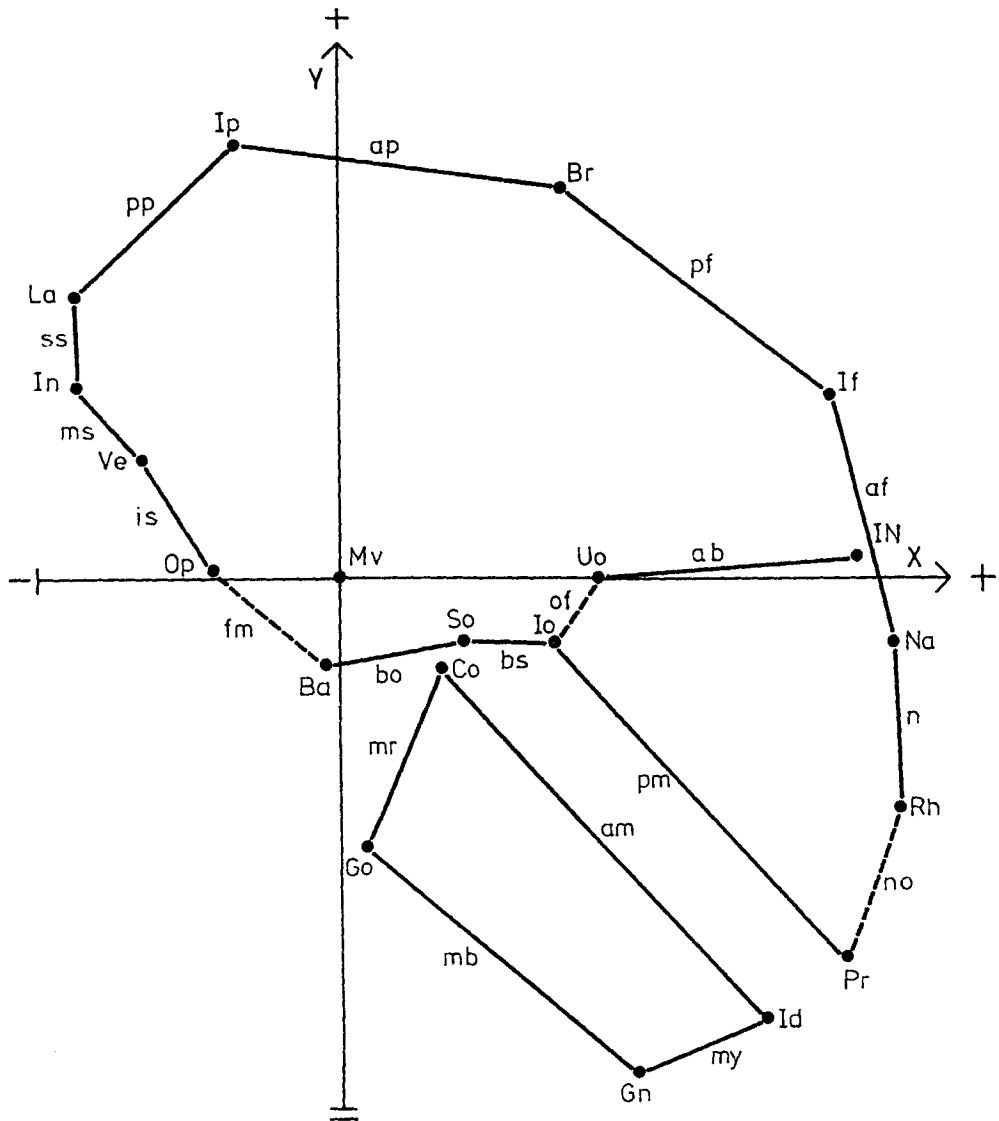


Fig. 1. Midsagittal tracing of the skull of an adult *Saimiri sciureus boliviensis* in vestibular orientation. Cranial points: Pr = prosthion, Rh = rhinion, Na = nasion, IN = inner nasion, If = interfrontal, Br = bregma, Ip = interparietal, La = lambda, In = inion, Ve = vermion, Op = opisthion, Ba = basion, So = supraoccipital, Io = infraoptic, Uo = supraoptic, Co = condyleon, Go = gonion, Gn = gnation, Id = infradental, Mv = mesovestibion. Chords: no = nasal opening,

fm = foramen magnum, of = optic foramen, n = nasal, af = anterior frontal, pf = posterior frontal, ap = anterior parietal, pp = posterior parietal, ss = upper squama, ms = mid squama, is = lower squama, bo = basioccipital, bs = basisphenoid, ab = anterior basicranium, pm = palatomaxillary vault, am = alveolo-mandibular border, mr = mandibular ramus, mb = mandibular body, my = mandibular symphysis. X = abscissa (vestibular line), Y = orthogonal through Mv.

TABLE 1. Mean ( $\bar{X}$ ) and standard deviation (SD) for the angles<sup>1</sup> of both C6 and C24 controls and the malnourished group (M24)

		C6		C24		M24	
Variable	Id. <sup>2</sup>	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
<b>Openings</b>							
Nasal	no	0.94	0.11	1.22	0.03	1.23	0.05
Foramen magnum	fm	5.43	0.03	5.51	0.05	5.55	0.04
Optic foramen	of	0.76	0.06	0.90	0.07	0.82	0.08
<b>Bones</b>							
Nasal	nb	1.51	0.04	1.61	0.02	1.66	0.10
Anterior frontal	af	1.66	0.04	1.78	0.07	1.73	0.07
Posterior frontal	pf	2.43	0.05	2.46	0.07	2.50	0.07
Anterior parietal	ap	3.01	0.04	2.98	0.06	3.08	0.05
Posterior parietal	pp	3.82	0.04	3.88	0.05	3.84	0.06
Upper squama	ss	4.58	0.05	4.70	0.09	4.74	0.03
Mid squama	ms	5.62	0.09	5.54	0.08	5.59	0.06
Lower squama	is	5.46	0.58	5.32	0.01	5.30	0.06
Basioccipital	bo	0.26	0.05	0.22	0.04	0.22	0.04
Basisphenoid	bs	6.21	0.10	6.23	0.08	6.25	0.07
Anterior basicranium	ab	6.23	0.06	6.36	0.07	6.33	0.14
Palatomaxillary vault	pm	5.41	0.05	5.44	0.05	5.47	0.05
Alveolomand. border	am	2.20	0.04	2.28	0.06	2.30	0.04
Mandibular ramus	mr	4.25	0.02	4.18	0.08	4.18	0.06
Mandibular body	mb	5.49	0.06	5.55	0.06	5.55	0.07
Mandibular symphysis	my	0.28	0.03	0.37	0.06	0.38	0.06

<sup>1</sup> Measured in radians.<sup>2</sup> Id. = abbreviated variable name.

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## RESULTS

### Angle variation

Mean and standard deviation values are given in Table 1. In controls, growth increased highly ( $P < 0.01$ ) the dimensions of the nasal opening, the anterior portion of the frontals, the upper occipital squama, the occipital and optic foramina, and the symphyseal portion of the mandible, and significantly increased ( $P < 0.05$ ) the nasal bones, the anterior basicranium, and the alveolar region of the mandible. A marked decrease was seen in the lower occipital squama. Undernutrition affected only the anterior portion of the parietal bones (Table 2).

### Length variation

Mean and standard deviation values are given in Table 3. In controls, growth greatly increased the dimensions of the nasal opening, the posterior portion of the parietals, the lower squama, the foramen magnum, the basioccipital bone, the palatomaxillary vault, and the alveolar, ramus, and body portions of the jaws. Growth significantly increased the nasals, the anterior basi-

cranium, and the mandibular symphysis. Growth also greatly decreased the upper squama of the occipital bone. Undernutrition greatly decreased the nasal opening, the anterior and posterior portions of the parietals, the basioccipital bone, and the anterior basicranium. Growth significantly affected the dimensions of the anterior frontal, lower squama, basisphenoid, palatomaxillary vault, and the mandibular ramus. Undernutrition also greatly inhibited the growth decrement of the upper squama (Table 4).

## DISCUSSION

Postweaning orthocephalization in *Saimiri sciureus* was evident because 10 out of the 19 segments measured (more than 50%) rotated by age. Variation was located in two main regions. One was the frontal-ethmoidal-facial region, involving the rostral half of the frontal bone, the nasal bone and nasal opening, the anterior basicranium, the optic foramen, and the alveolar and symphyseal borders of the mandible. The other was the foraminal-occipital region, involving the foramen magnum, and the upper and lower portions of the occipital squama. These two

TABLE 2. Multifactor analysis of variance for angles (radians)

Variable	Id. <sup>1</sup>	RDM age	RDM nutrition
<u>Openings</u>			
Nasal	no	12.96**	-0.41
Foramen magnum	fm	0.73**	-0.36
Optic foramen	of	8.44**	4.65
<u>Bones</u>			
Nasal	nb	3.21*	-1.53
Anterior frontal	af	3.49**	1.43
Posterior frontal	pf	0.62	-0.81
Anterior parietal	ap	-0.50	-1.65**
Posterior parietal	pp	0.78	0.52
Upper squama	ss	1.29**	-0.42
Mid squama	ms	-0.72	-0.45
Lower squama	is	-1.30**	0.19
Basioccipital	bo	-8.33	-8.33
Basisphenoid	bs	0.17	-0.17
Anterior basicranium	ab	1.03*	0.32
Palatomaxillary vault	pm	0.28	-0.28
Alveolomand. border	am	1.80*	-0.43
Mandibular ramus	mr	-0.83	0.00
Mandibular body	mb	0.54	0.00
Mandibular symphysis	my	13.85**	-1.33

<sup>1</sup>Id. = abbreviated variable name.\*  $P < 0.05$ .\*\*  $P < 0.01$ .TABLE 3. Mean ( $\bar{X}$ ) and standard deviation (SD) for the lengths (mm) of both C6 and C24 controls and the malnourished group (M24)

Variable	Id. <sup>1</sup>	C6		C24		M24	
		$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
<u>Openings</u>							
Nasal	no	8.4	0.7	10.9	0.4	9.5	0.3
Foramen magnum	fm	8.7	0.4	9.3	0.3	9.2	0.3
Optic foramen	of	5.1	0.1	5.0	0.2	5.0	0.3
<u>Bones</u>							
Nasal	nb	9.9	0.2	10.3	0.3	10.2	0.3
Anterior frontal	af	18.5	0.8	18.4	0.6	17.5	0.5
Posterior frontal	pf	21.9	0.8	21.4	0.7	21.3	0.7
Anterior parietal	ap	20.4	0.4	21.2	1.0	19.8	0.9
Posterior parietal	pp	13.5	0.2	15.5	0.5	14.0	0.5
Upper squama	ss	9.0	0.4	6.5	0.4	7.2	0.6
Mid squama	ms	7.3	0.8	6.6	0.5	5.9	0.5
Lower squama	is	7.8	0.6	9.2	0.4	8.6	0.6
Basioccipital	bo	8.6	0.8	9.7	0.3	8.6	0.3
Basisphenoid	bs	5.3	0.4	5.8	0.4	5.1	0.7
Anterior basicranium	ab	16.3	0.3	16.8	0.2	16.1	0.4
Palatomaxillary vault	pm	24.2	0.8	28.1	0.4	27.3	0.4
Alveolomand. border	am	27.3	1.1	31.0	0.2	30.2	0.8
Mandibular ramus	mr	11.8	0.9	12.9	0.4	12.2	0.5
Mandibular body	mb	20.1	0.8	23.4	0.8	22.8	0.4
Mandibular symphysis	my	9.2	0.8	9.9	0.5	10.2	0.2

<sup>1</sup>Id. = abbreviated variable name.

regions rotated around a third—basilar-parietal—which remained invariable (Fig. 2).

Orthocephalization in *Saimiri sciureus* was similar in shape—although not in intensity—to that of rodents. When the skulls of weanling rats were studied by the vestibular method, orthocephalization was formed by

three dynamic components: (1) the frontal-ethmoidal-facial complex, which rotates anterosuperiorly, (2) the parietal-sphenoidale (intermediate) region, which remains stable, and (3) the interparietal-occipital complex, which rotates posterosuperiorly (Pucciarelli, 1978).

TABLE 4. Multifactor analysis of variance for lengths (mm) (M24)

Variable	Id. <sup>1</sup>	RDM age	RDM nutrition
<u>Openings</u>			
Nasal	no	12.9**	6.9**
Foramen magnum	fm	3.5**	0.5
Optic foramen	of	-1.0	0.2
<u>Bones</u>			
Nasal	nb	1.6*	0.6
Anterior frontal	af	-0.3	2.4*
Posterior frontal	pf	-1.3	0.2
Anterior parietal	ap	1.9	3.4**
Posterior parietal	pp	7.0**	5.0**
Upper squama	ss	-16.3**	-5.3*
Mid squama	ms	-4.9	5.0
Lower squama	is	8.5**	3.8*
Basioccipital	bo	5.8**	5.8**
Basisphenoid	bs	4.7	6.0*
Anterior basicranium	ab	1.4*	1.7**
Palatomaxillary vault	pm	7.5**	1.4*
Alveolomand. border	am	6.4**	1.3
Mandibular ramus	mr	4.5**	2.7
Mandibular body	mb	7.6**	1.5
Mandibular symphysis	my	3.6*	-1.8

<sup>1</sup>Id. = abbreviated variable name.\*  $P < 0.05$ .\*\*  $P < 0.01$ .

Neural structures were found encompassed in the anterior-superior rotation of *Saimiri* and *Rattus*. This agrees with the relatively greater anteroposterior expansion of the frontal bone found by Corner and Richtsmeier (1992) in *Saimiri*. This suggests that orthocephalization is independent of any relative bone increment found in the vault. A further point of similarity between both genera was the stability of the intermediate region (parietal-sphenoidale in the rat and frontoparietal-occipitosphenoidale in *Saimiri*). The angular decrements of the upper segment of the squama in *Saimiri* followed the same interparietal-occipital rotation seen in the rat.

The flexion of the cranial base (Hill, 1960; Hershkovitz, 1977) must be considered as part of orthocephalization. The anterior basicranial region, despite its association with rostral structures (Moss and Vilmann, 1978), was considered here as formed by the segment between the upper border of the optic foramen and the tip of the cribriform plate (Delattre and Anthony, 1951). This region behaved differently than that defined by Virchow as "os tribasilare" (Moss and Vilmann, 1978) because of its sensitivity to the rotation of the frontal-ethmoidal-facial complex. A similar basal behavior was seen by

Scott (1958), who reported a close relationship between the anterior cranial base and the face. This kind of facial-anterior basal covariation agrees with the high growth rate of the upper face found in *Cebus* by Corner and Richtsmeier (1991). This also agrees with the active growing vomer-sphenoid junction recently seen in *Saimiri* (Corner and Richtsmeier, 1992). Our results also agree with the basicranial rotation in *Maca mulatta* reported by Michejda (1975) and by Sirianni and Swindler (1979), who observed that the anterior basicranium closely followed a dentofacial pattern, while the posterior portion grew according to demands of the growing brain.

Comparisons of our findings with those in pongids may be important since, according to Ameghino (1909), pongids and hominids resemble platyrrhine monkeys by groups of traits absent in cercopithecids. One of them is the position of opisthion. In *Saimiri* it practically coincides with the vestibular plane—slightly above, according to Delattre and Anthony (1951)—hence, the foramen magnum and the sella turcica are dragged to a subvestibular position (Fig. 2). Postero-cranial displacement was found in pongids (Fenart and Salmon, 1973). Counterclockwise rotation of the neural skull has been

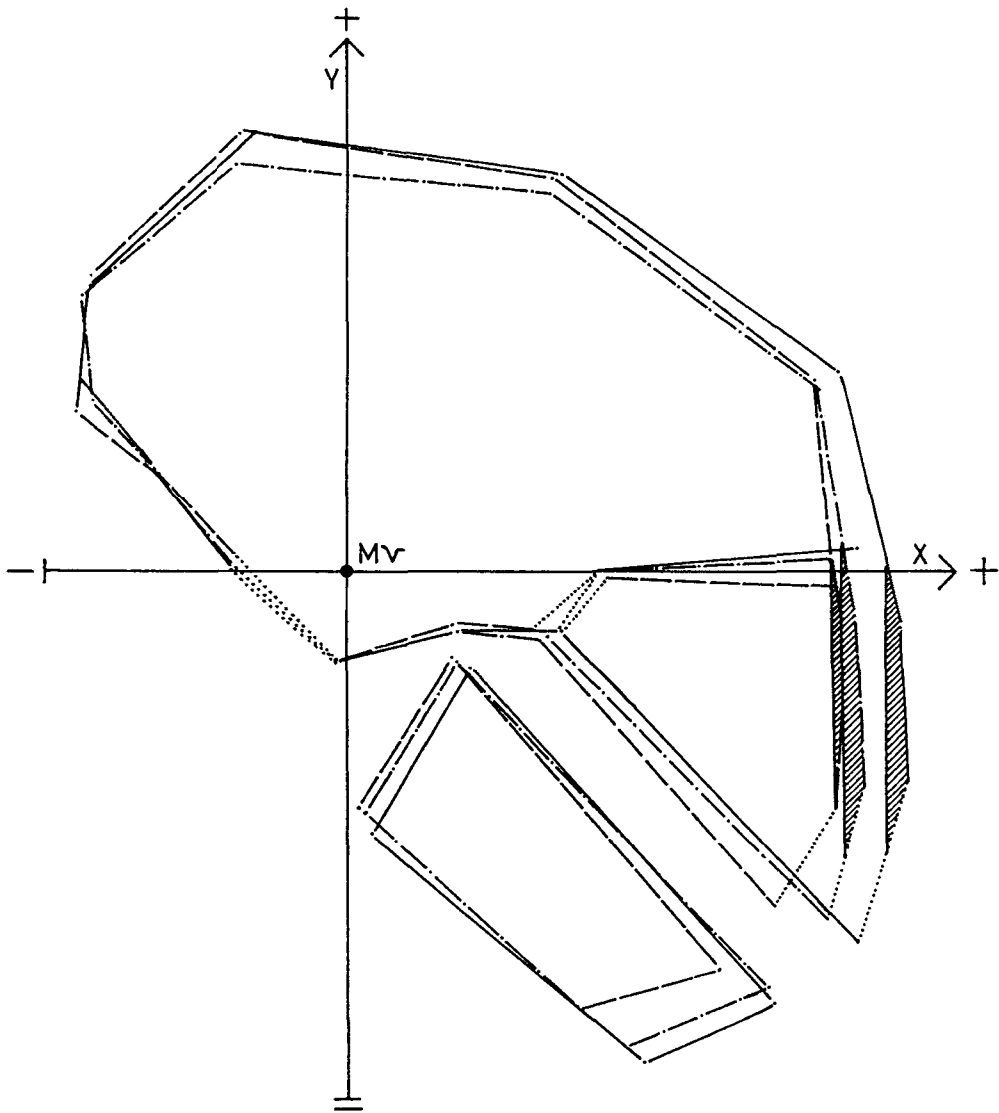


Fig. 2. Superimposed midsagittal tracings—according to the vestibular orientation—depicted from the mean coordinate values of the points. Dashed = C6 controls, dotted and dashed = M24 malnourished group, solid line = C24 controls. Mv = mesovestibion, X = abscissa (vestibular line), Y = orthogonal through Mv, hatched region = subvestibular prognathism.

reported by Delattre and Fenart (1960) for several nonhuman primates. These findings indicate that orthocephalization may also be present in apes.

The frontal-ethmoidal-facial rotation in *Saimiri* was mainly due to absolute and relative increments in the growth of the face. This was caused by the greater growth of

the palatomaxillary vault (and structures functionally associated with the masticatory apparatus). The greater increment of the nasal cavity (and structures functionally associated with the respiratory system) was also important.

Rotation is graphically shown by a vertical line passing through the intersection of the

vestibular plane with the frontal bone. In weaning animals, only the nasal and part of the anterior frontal bones were projected out of this vertical. The upper third of the nasal opening was also visible in the 24 month controls (Fig. 2). The facial movement observed here was contrary to the backward displacement of the palatal plane with respect to the orbitomandibular line. The same was described by Delattre and Fenart (1964) as part of the hominization of the skull.

Malnutrition affected growth in facial and/or neurocranial structures of apes and monkeys (Jha et al., 1968; Murchison et al., 1984; DeRousseau and Reichs, 1987; Pucciarelli et al., 1990; Dressino, 1991). The regions of greater growth—such as the nasals, the parietal and the basioccipital bones, the occipital squama, and the palatamaxillary vault—were mainly affected by malnutrition. This agreed with a previous cranial functional study made on the same species (Pucciarelli et al., 1990). Almost all angles remained constant in the stressed animals. It seems reasonable to conclude—agreeing with findings made in rats (Pucciarelli and Niveiro, 1981)—that postweaning undernutrition acts on growth in size but not on the shape changes of the *Saimiri* skull.

### CONCLUSIONS

1. Orthocephalization occurs in *Saimiri sciureus* and is still evident during the early postweaning growth period.
2. Malnutrition after weaning inhibits growth in size but not in shape.
3. Orthocephalization seen in *Rattus* and *Saimiri*, and inferred for pongids, suggests that this process is a general pattern of mammalian craniofacial development from which humans are not exempt.

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